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NOTES AND LITERATURE

SWINGLE[1] ON VARIATION IN F_1 CITRUS HYBRIDS AND THE THEORY OF ZYGOTAXIS

Swingle in two recent papers has published some very interesting observations on *Citrus* species and their F_1 hybrids. On the basis of these observations, the somewhat startling statement is made that current theories of heredity and variation give no adequate explanation of variability in F_1 hybrid generations from "pure bred" parent strains. Swingle assumes this variability to be so great that qualitative differences in chromosomes can not account for it. As the chromosomes in the F_1 hybrid remain unfused until synapsis, there is said to be no opportunity for quantitative exchange of hereditary substance, so that this variation can not be accounted for on this basis. Hence,

> if proof can be given to show that in certain specific cases, pairs of gametes of *identical hereditary composition*[2] give rise to very diverse organisms, the way has been opened for a general reinvestigation of the validity of our modern theories of heredity.

The term "pure bred" as used by Swingle implies that certain *Citrus* species reproduce themselves in a relatively faithful manner from seed, there being no overlapping of distinguishing specific characters and very little variation of these characters intraspecifically. *C. aurantium* and *C. trifoliata* are examples of such widely separated species. The former has been grown from seed in Florida for two hundred years, and though variations have appeared, they are said to differ but little from the general type of *C. aurantium,* and in no way to approximate that of *C. trifoliata.*

On the basis of evidence of this kind, Swingle believes the various *Citrus* species (*C. aurantium, C. trifoliata, C. medica limonum,* etc.) breed true in nearly all their characters and especially in those which differentiate them from one another. Hence, for genetic studies, the germ cells of these species are

1 Swingle, W. T., "Variation in First Generation Hybrids (Imperfect Dominance): Its Possible Explanation through Zygotaxis," IV° Conf. Internat. de Genetique, Paris, 1911, pp. 381–394; "Some New Citrus Fruits," *Amer. Breed. Mag.*, 4: 83–95, 1913.

2 The italics are my own.

assumed, in respect to these differential characters, to be pure; or, expressed in more technical language, each species is for the characters under observation, genotypically homozygous. This assumption is based on wholly inadequate evidence, as will be shown later.

Citrus trifoliata crossed with other *Citrus* species (*C. aurantium*, etc.) gave F_1 hybrid families showing a large degree of variability, even when the seeds from a single cross having identical male and female parents were grown. This variability expressed itself in foliage, habit of growth, and fruit, and was especially noticeable in the latter, the fruits of the F_1 individuals showing differences in color, size, texture, shape, number of seeds, and flavor. For example, from a single cross of *C. trifoliata* × *C. aurantium*, the 11 resulting hybrid seeds gave rise to F_1 plants (citranges) differing in foliage, habit of growth, and very strikingly in fruit. The fruit of one of these citranges, the "Morton," was smooth, round, very large, and orange-colored; those of the "Colman" were rather flattened, globose, pubescent, yellow, almost seedless, and lacked the disagreeable oil common to the others; while those of still another type, the "Willits," were often monstrously fingered. The "Phelps" was bitter, while the "Saunders" almost lacked this quality. The "Rustic" often has double fruits with many seeds, and a habit of growth more like its *aurantium* parent.

When varieties of the lemon were crossed with *C. trifoliata*, still greater differences in the F_1 generation (citremons) resulted. These consisted largely of "abnormal" foliage developments. Hypophylls, though absent in the common *Citrus* species are extremely characteristic of *C. trifoliata*. About 20 per cent. of the lemon-trifoliata hybrids developed an intensified form of this character, and this proportion occurred in each case in crosses involving three different varieties of lemon. The tangerine orange × grape fruit (tangelo) in the F_1 generation was almost as variable as the citrange families. F_1 hybrids between the West Indian lime and the kumquat (limequat) were strikingly different in such characters as aroma, flavor, acidity of pulp and thickness of skin.

Although much stress has been laid on the differences in these F_1 hybrids, there were numerous similarities. For example, all the *Citrus* hybrids involving *C. trifoliata* in their parentage have compound, semi-evergreen leaves, increased hardiness and fruits

with abundant bitterish, acid juice. Two of the citranges (Colman and Cunningham) have the pubescent fruit character of *C. trifoliata,* while the others are smooth-skinned.

The author's data led him to formulate in substance the following conclusions, which I have grouped and stated in my own language.

1. *Citrus* species are but slightly variable in the characters which differentiate them, and, in the sense that no overlapping takes place, may be said to breed true, their germ cells being genetically pure for these differential characters.

2. Individual plants of the F_1 hybrid generations between these species are strikingly variable, although all are, in a given cross, the zygotic product of *pairs of gametes* of "*identical hereditary composition.*"

3. Modern theories of heredity can not account for this variation.

These are not the conclusions, however, in which all present-day geneticists would concur. In the first place, few "modern" geneticists would take Swingle's view concerning the "pure breeding" ability of the various *Citrus* species, nor even of *C. aurantium.* Webber, in the Encyclopedia of American Horticulture, notes that 70 varieties of the common sweet orange are grown within our borders, and although a few varieties are fairly constant, the majority of these do not breed true from seed. Practically the same idea has been gained by certain prominent taxonomists of the genus *Citrus.* De Candolle specifically calls attention to the remarkable variability of the whole group; and Professor Hume of Florida remarks on the same fact in certain Experiment Station publications. As to the variability among the individuals in the special strains used by Swingle in his breeding work, no data are given, so that it can not be affirmed that inbred progeny from them would have been duplicates as far as hereditary characters are concerned. *Citrus* plants naturally cross fertilize, and from this cause alone no dependence can be placed on their ability to produce progeny, which are exact duplicates of themselves when inbred; in fact, the inference is that they would not. Hence, as far as intraspecific constancy of hereditary characters is concerned, Swingle's statement can not be accepted until more exact information is produced.

Swingle says no interspecific gradations occur between these various species, especially *C. trifoliata* and *C. aurantium.* Grant-

ing this, the two species have clearcut differences in leaves (evergreen or deciduous, unifoliolate or compound), in resistance to cold (difference in ability to withstand certain degrees of temperature) and in numerous fruit characters (presence or absence of pubescence, quality of juice, quantity of seed, size of fruit, etc.).

From the standpoint of modern theories of heredity as regards variation in F_1 hybrid generations, it matters little whether so-called species intergrade or whether their differences are clear-cut and all variation is intraspecific. In either case, if crosses were made, variation among the F_1 individuals from a single family might or might not occur. In either case, no violence to modern theories of heredity would result and no new problems would arise. But if two species that differ from each other in part or all of their characters, but breed true intra-specifically (genotypically homozygous) are crossed, and F_1 variation results, then modern theories of heredity would be compelled to change front and invoke the aid of new hypotheses. Swingle's data, assuming that intraspecific variation in *Citrus* species occurs, does not present a problem of this kind at all. *C. aurantium* and *C. trifoliata* each possess distinctive characters, but convincing data are not at hand to warrant any belief in the homozygosity of these differential characters or of even those the two species may have in common. The evidence directly, and one might almost say conclusively, opposes such a conclusion. If these species are not homozygous in all of their characters, then one can not affirm, in the light of modern theories, that all the gametes produced by a particular group of individuals called a species are identical in hereditary composition, nor even that the gametes of one individual of such a species are identical as to hereditary potentialities. At the risk of wasting valuable space by repeating what is extremely common knowledge to genetic students, let us assume, for the purpose of argument, that *C. aurantium* and *C. trifoliata* are homozygous in all their respective characters except one. In the former, the character A is heterozygous and peculiar to this species. Likewise, in *C. trifoliata*, B is heterozygous and differential. All the remaining characters of the two species may be symbolized, respectively, by the formulæ XX and YY. When $XXAabb$ (*C. aurantium*) is crossed with $YYaaBd$ (*C. trifoliata*), the resulting progeny would appear in the approximate proportion of $1\,XYAaBb : 1\,XYAabb : 1\,XYaaBb : 1\,XYaabb$, providing

A and B are single factor characters. In the majority of characters, the F_1 hybrids would be intermediate or possess those of either one or the other parent, since all the F_1 individuals would be alike as far as any hereditary quality symbolized by XY is concerned, providing the plants were all grown under the same environmental conditions. But these F_1 individuals would not be alike as regards the inheritance of the characters A and B. Experimental evidence from crosses of this kind show us that four different F_1 forms may result, the distinctions between them arising from the presence or absence, through inheritance, of the characters A and B. Dominance is assumed to be absent in this illustration.

Swingle's *Citrus* hybrids, though involving greater complexity because a large number of parental characters instead of two are probably heterozygous, are of the same general type as those of the illustration and lend themselves to the same interpretation. Owing to the absence of sufficient exact experimental data, one can not speak of unit characters and factors in these hybrids, but one may say without violence to modern theories of heredity that one or both of the parents involved in the crosses which produced the Colman and the Cunningham were heterozygous in the factors or factor for pubescence, that various size factors were heterozygous and that one parent was homozygous for absence and one for presence of the factors for hardiness, compound leaves and evergreen foliage.

F_1 variation in *Citrus* hybrids then, in the light of the data at hand, apparently results from differences in the gametic composition of the heterozygous parents.

Swingle calls attention to other cases of variation in F_1 hybrids from two pure stocks which support his contention that this phenomenon of F_1 variation is very general, though usually obscured through variation due to heterozygous parent stock. Collins and Kempton[3] crossed a race of corn breeding true to waxy endosperm with one constant for horny endosperm. Horny endosperm was dominant in F_1 and the F_2 generation segregated in the expected ratio of 1 waxy to 3 horny kernels. This ratio represented the average proportion of each when the ears of all the plants were lumped together. The F_2 progeny of each selfed

[3] Collins, G. N., and Kempton, J., II, 1912, "Inheritance of Waxy Endosperm in Hybrids of Chinese Corn," IV° Conf. Internat. de Genetique, 1911, p. 347; also Circ. No. 120, Bur. of P. I., U. S. Dept. of Agr., 1913.

F_1 plant when taken by itself gave some ears as low as 13.7 per cent. waxy, while others exceeded the expected proportions and gave ears as high as 33.3 per cent. waxy. The investigators point out that this variation is not the result of the laws of chance as the deviation is far greater in many cases than the probable error. Therefore, says Swingle,

> there can be no doubt but that their varying percentages represented real differences in the hereditary composition of the first generation plants. It would be hard to find a more conclusive case since there could be no doubt as to the purity of the parents and what is more rare no possible doubt as to whether a given kernel had a waxy or a horny endosperm.

Mendelians are said to be unaware how fatal this phenomena is to some of the chief tenets of modern theories of heredity, and they are also accused, somewhat unjustly, I believe, of applying the term "imperfect dominance" to this and to the *Citrus* phenomena.

In this case, both parents were undoubtedly homozygous for their respective endosperm characters, so that heterozygosity will not account satisfactorily for the deviations. But this is a different phenomena than Swingle found in his *Citrus* hybrids, for here one is dealing with a fluctuation in a proportion or ratio involving the same character, while in his experiments the difficulty was the variation in presence and absence of distinct and often new characters, indicating an extremely heterozygous parentage.

As an explanation or working hypothesis for his own and similar data, Swingle advances a somewhat new and suggestive chromosome theory on the assumption that it fills an urgent need. The theory of zygotaxis, as it is called, may be summarized as follows:

Maternal and paternal chromosomes probably persist side by side in the cells, unchanged in quality and number throughout the whole development of the F_1 organism. This being true, Swingle, in order to explain his data, assumes that the influence in character formation exerted by chromosomes on the F_1 hybrids, is in some cases due to their relative positions in the nucleus, and that these relative positions result from accident or at least are determined at the moment of nuclear fusion in fertilization, and remain unchanged in succeeding cell generations. He further

assumes that those chromosomes lying nearest the nuclear wall (peripheral) are better nourished than those centrally located, and hence they exert more influence in character formation, and dominating synapsis, produce gametes similar in their hereditary character to the cells of the first generation hybrids, whose character in turn was determined at fertilization by the configuration the chromosomes took in the fusion nucleus. On this theory, reversions, sports, etc., may result from sudden changes in the nuclear configuration.

Three types of nuclear configuration are assumed to occur in higher organisms, the character and effects of which are synoptically outlined below.

1. *Interspecific Hybrids.*—Usually sterile and intermediate. Chromosomes repel each other and occupy opposite sides of the F_1 zygote nuclei, exerting equal influence in the ontogeny of F_1 organisms, explaining why first generation hybrids of this character are always intermediate, little variable and usually sterile. Synapsis often impossible.

2. *Mendelian Crosses.*—Abnormally inbred races of domesticated animals and plants. F_1 generation usually intermediate, fertile, dialytic at synapsis. Dominance of certain characters in these hybrids is due to the inherited potentialities of the chromosomes rather than to their nuclear positions.

3. *Normal Cross-bred Species.*—Probably normal in wild species. Hybrids usually vigorous, fertile, and variable. Free intermingling of chromosomes in the fusion nucleus at fertilization. Nuclear configuration permanent for each individual. Synapsis normal.

This elaborate and attractive theory, based admittedly to a great degree on assumptions, is advanced by Swingle in the belief that it will help to clarify the problems of heredity, even though he acknowledges it does not help one to arrive at satisfactory explanations. In the reviewer's opinion, however, the field of genetics is already burdened with enough theories of this particular type and the somewhat unnecessary but ever-increasing new additions serve to confuse rather than clarify the ideas of the average student of genetics. Besides, Swingle's assumption that maternal and paternal chromosomes in the cells of F_1 hybrids repel each other and do not mingle in the F_1 zygote cells is not borne out by the few cytological facts at our command. Rosen-

berg's[3] work on species hybrids of *Drosera*, Moenkhaus's[4] investigations of species hybrids in fish and some work on certain hybrids in the Echinodermata group give us facts that directly oppose such an assumption. As a further criticism, one may say that most biologists who have had experience with pedigree cultures would decidedly criticize the synoptic outline and the narrow sphere assigned to Mendelian phenomena.

Aside from the theoretical considerations, these two papers contain descriptions of *Citrus*-like species new to occidental horticulture, together with a somewhat detailed account of the various *Citrus* hybrids and their hardiness and practical value, showing the truly fine results achieved by the workers in this field toward moving the *Citrus* belt northward and adding *new* varieties of this genus to the world's horticulture.

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BROOKLYN BOTANIC GARDEN,
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[3] Rosenberg, O., "Cytologische und Morphologische Studien an *Drosera longifolia* × *D. rotundifolia*," Kungl. Svenska Vetenskapsakademiens Handlinger., 43, N: ou, pp. 1–64, 1909. 4 Tafn.

[4] Moenkhaus, W. J., "The Development of the Hybrids between *Fundulus heteroclitus* and *Menidia notata* with especial reference to the Behavior of the Maternal and Paternal Chromatin," *Amer. Jour. of Anatomy*, 3: 29–65, 1904. Plates I–IV.